

A NEW *PLATANThERA* (ORCHIDACEAE) FROM YOSEMITE NATIONAL PARK, CALIFORNIA

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ABSTRACT

A new species, *Platanthera yosemitensis* Colwell, Sheviak and P. Moore, from Mariposa County, California, is described and illustrated. Endemic to wet montane meadows between the main stem and the South Fork of the Merced River in Yosemite National Park, it is distinct from *Platanthera stricta* Lindl., *P. sparsiflora* (S. Wats.) Schlechter, and *P. purpurascens* (Rydb.) Sheviak & W. F. Jennings based on vegetative habit, floral morphology, color, and fragrance and pollination mechanics.

Key Words: California, Orchidaceae, *Platanthera*, Sierra Nevada, Yosemite National Park.

The central Sierra Nevada of California supports a small number of *Platanthera* species, including *P. dilatata* (Pursh) Lindl. ex Beck var. *leucostachys* (Lindl.) Luer, *P. sparsiflora* (S. Wats.) Schlechter, *P. stricta* Lindl., and *P. tescamnis* Sheviak & Jennings. *Platanthera purpurascens* (Rydb.) Sheviak & W. F. Jennings was also reported from the central Sierra Nevada of California (Coleman 1995; Sheviak 2002) based on a fragmentary specimen. The range of *P. purpurascens* is otherwise limited to the southern Rockies from southernmost Wyoming to south-central New Mexico and eastern Arizona. The anomalous, disjunct nature of the putative California record stimulated our investigation, which determined that the record was based not on *P. purpurascens* but rather represented an undescribed, endemic species.

DESCRIPTION

Platanthera yosemitensis A. Colwell, C. Sheviak and P. Moore, sp. nov. (Fig. 1). TYPE: USA, California, Mariposa County, Yosemite National Park, northeast of Badger Pass Ski Area, 37°39'N, 119°39'W, 2200 m. Wet meadow with *Platanthera dilatata* var. *leucostachys* Lindley, *Platanthera sparsiflora* (S. Watson) Schltr., *Polygonum bistortoides* Pursh, *Gentianopsis simplex* (A. Gray) Iltis, *Mimulus primuloides* Benth., *Spiranthes romanzoffiana* Cham. Flowers greenish yellow,

strongly sweet-spicy-musk scented. 30 July 2003, A.E.L. Colwell & C. Coulter 03-33. Holotype: UC 1861834; Isotypes: NYS A33130, YM 117815.

Folia 5–7 prope basin caulis plerumque (suprema infra medium) inserta, supra bracteis redacta. Folium infimum reflexum, ceterum perascendens, 9–25 × 1.5–3 cm. Spica laxa florifera, longitudine 1/2 caulis partes aequantia, aliquantum glauca. Sepalum dorsale viride vel margine flavescenti, porrectum. Sepala lateralia viride reflexa. Corolla citrina. Labellum rhombilanceolatum, saepe basi plus minusve rotundatidilatata, apice plerumque apicem sepalii dorsalis contingenti, interdum libero, labellum tum horizontale, 4–6 mm longum. Calcar saccatum vel scrotiforme inflatum e basi tenui. Columna parvula rotundata, connectivum angustum sed evidens, anthera sacculis parallelis vel aegre divergentibus, lobis rostellii brevissimis prope marginem superiorem orificii calcaris terminantibus. Viscidia orbiculati-quadrata.

Perennial herb, 20–80 cm tall, composed of a single stalk from a horizontal tapered tuberoid and a few fleshy roots, the bud for the subsequent year forming near the base of the current year's stalk on a newly developing tuberoid. Stem stiff and round with minute longitudinal ridges. Leaves 5–7 on the lower 2/5 of stem; Lowest leaf reflexed, ca. 4 cm long × 1 cm wide, the others short-sheathed, clasping, three-nerved, conduplicate, lanceolate, strongly ascending, tapering to an acute, naviculate tip, 9–25 cm long, 1.5–3 cm wide, reduced above to clasping bracts. Inflorescence a lax spike along the upper half of the stem,

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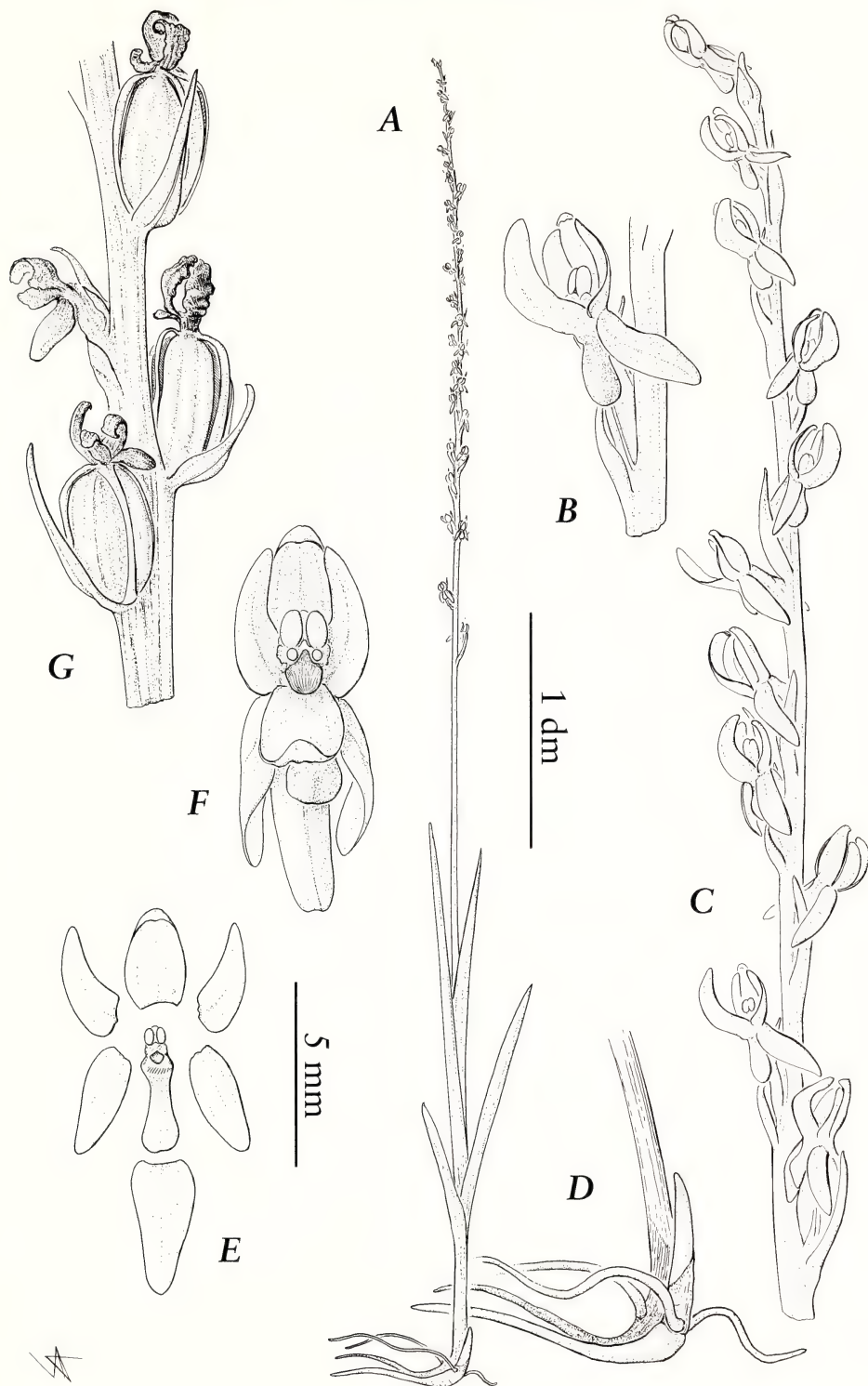


FIG. 1. *Platanthera yosemitensis*. A. Habit; B. Side view of flower; C. Detail of inflorescence; D. Root system; E. Dissected view of flower; F. Front view of flower; G. Detail of mature fruit. Illustration by John Myers.

somewhat glaucous on rachis, floral bracts, and flowers. Flowers 30–50, sparsely arranged in an irregular spiral, floral bracts attenuate, 1-nerved, approximately equaling the ovary. Flowers sessile, resupinate, gradually diminishing in size upwards and the uppermost generally not developing mature fruit. Dorsal sepal green or the margins yellowish, ovate, porrect, partially enclosing and connivent with the petals to form a hood. Lateral sepals green, oblong, slightly tapered to tips, reflexed downwards along the sides of the ovary. Corolla yellow, the segments thick, entire. Petals falcate, obliquely dilated at the base, asymmetrically ovate-deltoid, the upturned obtuse apices approximate, (3–) 4 mm long. Lip rhombic-lanceolate, the base often somewhat rounded-dilated, the apex commonly connivent with the apex of the dorsal sepal, sometimes free and the lip then horizontal but not descending, (4–) 6 mm long. Spur saccate or scrotiform, expanding from a more slender base, (2.0–) 2.8 mm long. Column very small, rounded, the anther erect, connective narrow but evident, anther sacs parallel to slightly diverging, rostellum lobes very short, obscure, the orbicular-quadrate viscidia held above the orifice of the spur. Fruit a stout cylindric capsule, 1 cm long in lowest flowers, diminishing in size upwards to 0.3 cm. Perianth persistent on the capsule apex but shriveling and darkening upon drying.

Chromosome number. $2n = 42$ (C. Sheviak, A.E.L. Colwell, & A. Sanders 6998 [NYS A33490], from 3 inflorescences collected at same site as A.E. L. Colwell & C. Coulter 03-33).

Flowering period. July–August.

Etymology. This species is named for Yosemite National Park, to which it appears to be endemic (Fig. 2). We suggest the common name Yosemite bog-orchid.

Paratypes. USA, California, Mariposa County: Yosemite near Glacier Point, 14 July 1923, *George Henry Grinnell s.n.* (RSA 382940); Meadow above Chinquapin on road to Glacier Point, 14 July 1923, *George Henry Grinnell* 123 (RSA 382932); Badger Pass, Yosemite National Park, *Mary V. Hood, s.n.* 6 August 1965 (YM 117456); Yosemite National Park, off Glacier Point Road, 14 Jul 1993, *R.A. Coleman s.n.* (NYS A12358); Yosemite National Park, Meadow Brook, 37° 41'N, 119°39'W, 2158 m, 24 July 2003, *A.E.L. Colwell & C. Coulter* 03-22 (YM 117810); Yosemite National Park, Meadow Brook, 37°41'N, 119°39'W, 2158 m, 20 August 2003, *A.E.L. Colwell & C. Coulter* 03-46 (YM 117804); Yosemite National Park, Meadow near Glacier Point Road, 37°39'N, 119°39'W, 2225 m, 13 August 2004, *A.E.L. Colwell & A. Sanders* 04-238 (MO 04479050); Yosemite National Park, Rail Creek, 37°39'N, 119°40'W, 2200 m, 26

September 2004, *A.E.L. Colwell & P. Moore* 04-306 (YM 118100).

DISCUSSION

Distribution and Habitat

Platanthera yosemitensis is currently known from only nine sites within Yosemite National Park, all on the granitic upland south of Yosemite Valley, within 4 km of Monroe Meadows (Fig. 2). As the range is currently known, it is the only orchid species endemic to the Sierra Nevada in California. Its habitat is wet meadows between 2100 and 2285 m elevation in partial shade cast by a surrounding forest of *Abies magnifica* Andr. Murray and *Pinus contorta* Loudon. These meadows are at headwaters of first order streams in steep terrain with forested watershed above them. *Platanthera yosemitensis* occurs within these meadows in sites of active groundwater seepage. Individuals are found in well-developed turf with dense (<1 m tall) herbaceous vegetation, often dominated by *Carex utriculata* Boott, *Dodecatheon alpinum* (A. Gray) E. Greene, *Eleocharis pauciflora* (Light.) Link, *Luzula subcongesta* (S. Watson) Jepson, *Pedicularis attolens* A. Gray, *Perideridia bolanderi* (A. Gray) Nelson & J. F. Macbr., *Phalacroseris bolanderi* A. Gray, and *Polygonum bistortoides*.

The upland area south of Yosemite Valley inhabited by *P. yosemitensis* is noteworthy because it contains several species endemic to the central and southern Sierra Nevada: *Allium yosemitense* Eastw., *Eriophyllum nubigenum* A. Gray, *Hulsea brevifolia* A. Gray, *Ivesia unguiculata* A. Gray, *Senecio clarkianus* A. Gray, *Phalacroseris bolanderi*, and *Trifolium bolanderi* A. Gray. Age and stability of this montane habitat and hence of the composition of the regional species pool (Millar and Woolfenden 1999) is likely a factor related to this level of endemism. This upland remained largely free of ice during the most recent glacial events that scoured much of the Sierra Nevada and carved the valleys to the north and south in the last two million years (Matthes 1930; Alpha et al. 1987). Matthes (1930) infers that, during periods of glacial maxima, this exposed surface was not forested, but was instead covered by an alpine meadow that had seasonal snow cover as the area does currently. The current habitat of *P. yosemitensis* is similar to the habitat described by Matthes and to modern day periglacial environments.

In addition to harboring glacial refugia during the Pleistocene, recent geologic evidence suggests that montane habitat in the Sierra Nevada is significantly older (Small and Anderson 1995; Wernicke et al. 1996; Stock et al. 2004, 2005;

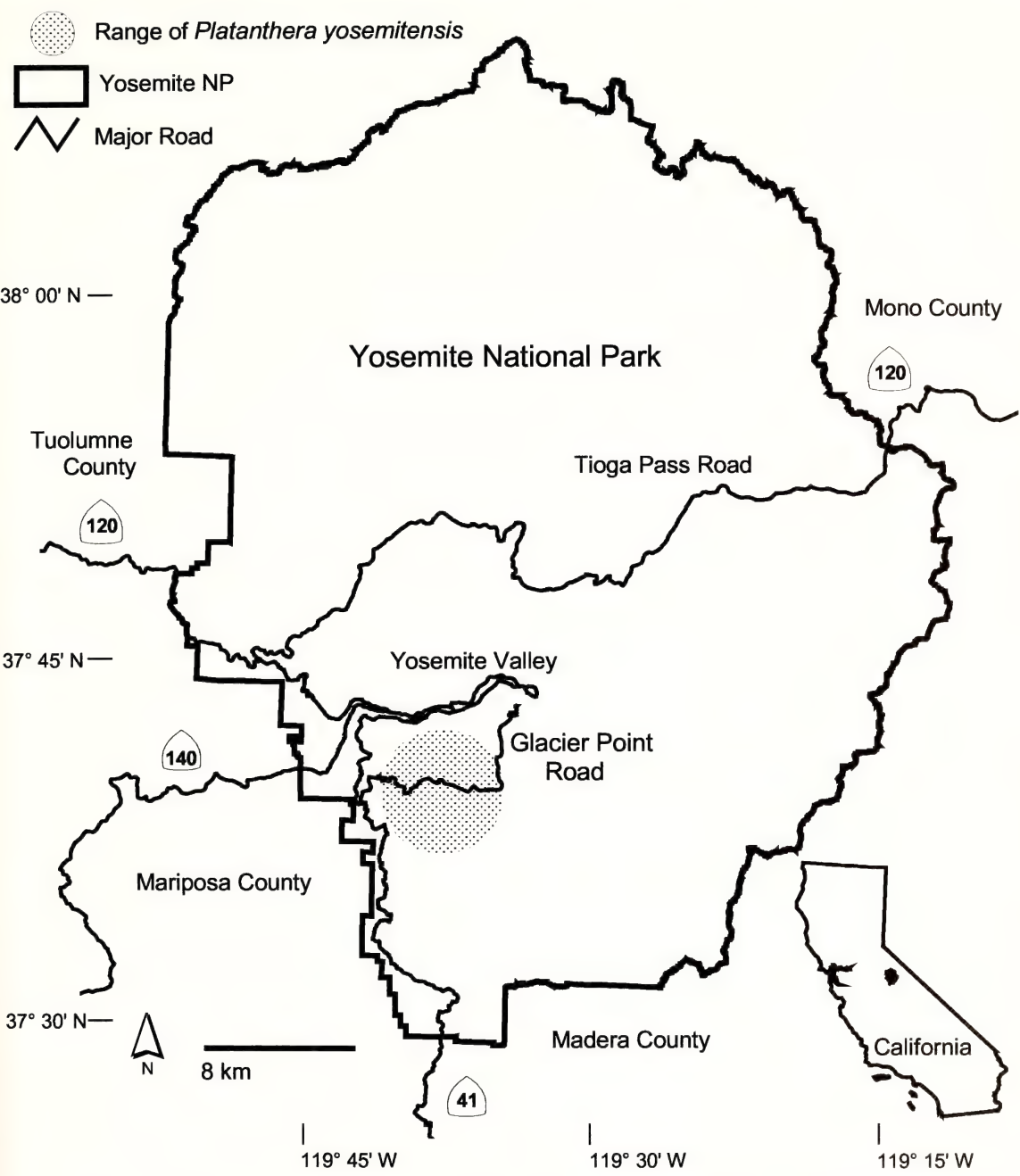


FIG. 2. Range of *P. yosemitensis* in Yosemite National Park, central Sierra Nevada, California.

Mulch et al. 2006), than the few million years previously accepted (Sharsmith 1940; Chabot and Billings 1972; Raven and Axelrod 1978). House et al. (1998, 2001) propose a Cretaceous origin of high elevation mountains in the southern Sierra Nevada. Stock et al. (2005) present evidence that some Sierra Nevada uplands have been eroding very slowly, only about 10 m per million years. Stable montane habitat on the order of tens of

millions of years in age should be thought of as a site of in situ speciation of montane plants (Kimball et al. 2004). In this context, the discovery of a distinct orchid species is not surprising and the distribution of *P. yosemitensis* may well be more widespread within this region than is currently known. It should therefore be sought in similarly unglaciated wet meadow sites elsewhere in the central Sierra Nevada.

Taxon Relationships

The *Platanthera* species of the central Sierra Nevada of California include *P. dilatata* var. *leucostachys*, *P. sparsiflora*, *P. stricta*, and *P. tescamnis*. They are part of a transcontinental complex of species long noted for taxonomic intractability. They are not readily determined by superficial examination of gross morphology, but rather require careful study of certain critical characters, especially of the column.

Platanthera sparsiflora has typically been recognized on the basis of a large column filling much of the hood formed by the sepals and petals. More significantly, the viscidia, the sticky pads that affix the pollinaria to the pollinator, are borne on prominent, angular rostellum lobes that present them forward and to either side of, or somewhat below, the orifice of the spur. The connective, the sterile tissue between the anther sacs, is correspondingly very broad. The column is typical of those of *Platanthera* species that place pollinaria on insects' eyes. This configuration is seen in the types of *P. sparsiflora* and its taxonomic synonyms, *Limnorchis laxiflora* Rydb., *Limnorchis ensifolia* Rydb., and *Habenaria aggregata* Howell (See Sheviak & Jennings [2006] for discussion and illustration of types.). The more eastern *P. zothecina* (Higgins & Welsh) Kartesz & Gandhi, of the Colorado Plateau, bears a functionally similar column, but it is not clear if it reflects a common origin or a parallel or convergent development.

In contrast to the broad, angular-lobed column of *P. sparsiflora*, the columns of the other species in the region are small, with abbreviated, more rounded rostellum lobes that present the viscidia closer to the orifice of the spur, typically near the upper margin. Pollinaria are thus placed on the proboscis or mandibles or on the eyes of smaller insects. Among these species, *P. dilatata* var. *leucostachys* is distinguished by its pure white, nocturnally fragrant flowers with slender spurs much longer than the lips. The remaining species bear flowers more or less green or greenish yellow in general aspect. These include the recently described *P. tescamnis* which is discussed at length by Sheviak & Jennings (2006). For purposes of the present discussion, *P. tescamnis* is recognized by a slender to slightly clavate spur somewhat shorter to slightly longer than the lip. The remaining species bear comparatively short, inflated spurs.

Platanthera purpurascens was recently reported from the central Sierra Nevada of California (Coleman 1995; Sheviak 2002) based on a determination by Sheviak of an inflorescence fragment. This species was originally described over a century ago as one of Rydberg's species of *Limnorchis* (Rydberg 1901). Ames (1910) reduced it to varietal status under *Habenaria hyperborea*

(L.) R. Br., but subsequently it was largely ignored, even in synonymy, until treated as a variety of *Platanthera hyperborea* (L.) Lindl. by Luer (1975). In the intervening years it had been confused with *P. stricta* Lindl., with which it shares a short, scrotiform or saccate to inflated-clavate spur. This single-character taxonomy is analogous to the recognition of *P. sparsiflora* based on its large column; in both cases, the character reflects a pollination syndrome and is a reliable indicator of neither evolutionary history nor relationship (Sheviak 2002). Of greater significance is the similar vegetative habit of *P. stricta* and *P. purpurascens*. The leaves of both species are relatively short, blunt, commonly widely spaced, and abruptly diverging from the stem, often at nearly 90 degrees. Plants of both species are commonly slender, with long, lax inflorescences, but robust plants can be more densely flowered. However, the two species differ significantly in other details, most significantly in column shape and floral fragrance, and less definitively in flower color and lip shape. In the column of *P. stricta*, the anther sacs and rostellum lobes are approximately parallel or somewhat converging. In contrast, in *P. purpurascens* they are wide-spreading. Flowers of *P. stricta* are scentless or rarely with the faintest hint of a spicy scent; those of *P. purpurascens* are strongly musty scented. These two characters evidently reflect different pollination specializations that would be of species-level significance. Additionally, flowers of *P. stricta* are typically a concolor medium green, with linear oblong lip of the same hue as the rest of the flower. The lip may vary occasionally toward more lanceolate and, in the North, yellowish, but the species is much more uniform than is *P. purpurascens*. In *P. purpurascens*, populations commonly show considerable variation with lip linear lanceolate to broadly rounded-dilated at the base, and varying in color from markedly bluish green to dull yellowish; sometimes it is marked with reddish blotches, hence the specific epithet.

Platanthera yosemitensis differs from *P. stricta* and *P. purpurascens*, the other species with scrotiform-saccate spurs, in vegetative habit. In contrast to the wide spacing and typically abrupt spreading of the rather short, blunt leaves of *P. stricta* and *P. purpurascens*, those of *P. yosemitensis* are long, tapered, ascending, and clustered at the base of the stem. The long, lax inflorescence is then borne on a sparsely-bracted scape.

Flowers of *P. yosemitensis* and *P. purpurascens* show limited similarity. In addition to the spurs, the lanceolate lip, and orbicular to orbicular-quadrangle viscidia characteristic of *P. yosemitensis* are typically, if not uniformly, seen also in *P. purpurascens*. A dilation of the base of the lip is common in *P. yosemitensis*, and is sometimes

found in *P. purpurascens*, where it is much less common, but may be more strongly developed. Otherwise, the species differ markedly.

The rachis, floral bracts, pedicellate ovary, and abaxial surfaces of the sepals of *P. yosemitensis* are somewhat glaucous, a condition unique in the genus. Only the very large-flowered *P. zothecina* of the Colorado Plateau is superficially similar in the whitish-green cast of its inflorescence. In that species, however, the whitish coloring is not so much a glaucous bloom as a general pale coloration. Perhaps as a consequence of this glaucous surface, flowers of *P. yosemitensis* persist in a blackened, shriveled state atop the expanded capsules, lending a distinctive aspect to the plant after flowering.

Platanthera yosemitensis is furthermore unique in its concolor rich yellow corolla. In other species with yellowish lips, the hue is more suffused with green or rather dull, and the petals are green or greenish. The clear color throughout the corolla in *P. yosemitensis* is notable. The scrotiform-saccate spur is essentially an extreme development of the inflated-clavate form seen occasionally in *P. stricta* and *P. purpurascens*, pendulously inflated from a short slender base. Whereas saccate spurs in *P. stricta* and *P. purpurascens* are more nearly sessile on the base of the lip, and the more clavate extreme is merely a blunt inflation of a generally tubular structure, in *P. yosemitensis* the nearly spherical sac is born on the summit of a distinct expanding tube.

Platanthera yosemitensis has a pronounced fragrance with a prominent musk component. It has been likened by different observers to a corral of horses, asafoetida, strong cheese, human feet, sweaty clothing, or simply disagreeable. It is similar to the scent of *Polygonum bistortoides*, a frequent component of the meadows *P. yosemitensis* inhabits. Other similar species vary from strongly spicy of cloves (*P. dilatata* vars. *dilatata* and *leucostachys*), sweetly pungent (*P. dilatata* var. *albiflora* (Cham.) Ledeb., *P. huronensis* (Nutt.) Lindl., most *P. tescamnis*, some *P. aquilonis*, etc.), or strongly musty (*P. purpurascens*), to entirely or virtually scentless (*P. stricta*, *P. sparsiflora*; Coleman's report [Coleman 1988] of a sweet scent in the latter was the result of an editing error, [Coleman pers. com.]). The combination of scent, the yellow color and the short distance between the viscidia (0.3 mm) in *P. yosemitensis* may be indicative of a mosquito or fly pollination syndrome, which is also reported from the much larger-flowered *P. obtusata* (Raup 1930; Stoutamire 1968; Thien 1969; Gorham 1976).

Platanthera yosemitensis is consistent in vegetative and floral morphology, floral color, and scent, displaying only limited variation. One feature of *P. yosemitensis* is its uniformity of character expression within and between popula-

tions. Although its limited distribution might be taken to explain its greatly limited variability, in other *Platanthera*, especially *P. purpurascens*, great variability is commonly seen within even small colonies.

Hybrid formation in *Platanthera* is frequently reported, and is suspected between *P. yosemitensis* and sympatric species. *Platanthera sparsiflora* and *P. dilatata* var. *leucostachys* are common in the same meadows in which *P. yosemitensis* is found. A single plant in each of two *P. yosemitensis* populations appears to have floral characters intermediate between *P. yosemitensis* and *P. sparsiflora*. Phenology provides some measure of isolation as *P. sparsiflora* blooms earlier and is generally in fruit set by the time *P. yosemitensis* plants begin flowering. Furthermore, the different column structures and resulting differences in placement of pollinaria suggest that such crosses must be very rare and are probably the result of exploration by generalist pollinators rather than a properly oriented vector. Similarly, two plants at one site were intermediate in color and morphology between *P. yosemitensis* and *P. dilatata* var. *leucostachys*. Hybridization between these species again would appear to be rare due to the totally incompatible spur lengths. Nonetheless, random visitation by non-adapted insects might more frequently result in hybridization of these species than of *P. yosemitensis* with *P. sparsiflora* because the columns of *P. yosemitensis* and *P. dilatata* are similarly proportioned.

Platanthera dilatata var. *leucostachys* and *P. sparsiflora* often fill all the fruits on their inflorescences. In contrast, *P. yosemitensis* generally matures only the fruits on the lower two-thirds of the inflorescence. A few individuals have been found with all fruits filled, but others, especially those in small populations or on the margin of a population, fill only one or two fruits on an inflorescence. When this is the case, the filled fruits are not necessarily the lowest fruits, or even adjacent to each other on the inflorescence stalk, implying that this species is not self-pollinating.

Conservation Status

All of the known occurrences of *P. yosemitensis* are within the boundaries of Yosemite National Park. It is likely that additional occurrences will be found in the vicinity, especially to the south. Of nine known occurrences, five are located in remote areas, while four are adjacent to areas of frequent human use. The delicate inflorescence of this species is difficult to discern in the dense meadow vegetation in which it grows, which makes *P. yosemitensis* less likely to be noticed or poached. A greater concern is the small number of individuals at most of the sites (at four sites, fewer than ten flowering individuals

TABLE 1. CHARACTERS OF THE CALIFORNIA *PLATANATHERA* SPECIES.

Species	<i>P. dilatata</i> var <i>leucostachys</i>	<i>P. sparsiflora</i>	<i>P. stricta</i>	<i>P. tescamnis</i>	<i>P. yosemitensis</i>
Spur shape	Slender to cylindric	Slender to cylindric	Club-shaped to scrotiform	Clavulate (cylindric)	Scrotiform
Spur length	Greater than 1.5× lip length	Approximately 1× to approximately 1.5× lip length	Approximately 0.25× to less than 1× lip length	0.8 to 1.4× lip length (much less in some scentless plants)	Less than 0.5× lip length
Flower color	White	Green	Green (lip sometimes marked with small areas of fine reddish venation)	Green (lip greenish yellow to yellowish)	Yellow
Scent	Strong spicy	None	None (rarely faintly spicy)	Sweet pungent or none	Strong musk
Viscidia placement	Above spur orifice	Either side of spur orifice	Above spur orifice	Above spur orifice	Above spur orifice
Viscidia shape	Linear to linear-oblong	Orbicular to oblong	Orbicular	Orbicular or oblong	Orbicular-quadrate
Leaf shape	Lance-elliptic to linear elliptic	Lance-elliptic to linear elliptic	Oblong to ovate-lanceolate	Lance-elliptic to linear elliptic	Lance-elliptic to linear elliptic
Leaf orientation	Ascending to gradually arching, internodes obscured	Ascending to gradually arching, internodes spreading or abruptly exposed	Abruptly spreading, internodes exposed	Ascending to gradually arching, internodes obscured	Ascending to gradually arching, internodes obscured

have been observed), which are at risk of extirpation due to random natural events as well as anthropogenic threats. In order to protect these populations, location details have been left out of the specimens cited above. All of the known sites are in meadows exhibiting encroachment by *Pinus contorta*, a regional phenomenon in the central Sierra Nevada (Millar et al. 2004), which may pose a long-term threat to these populations. Active management may thus eventually be required to insure the species' survival.

The similarity of early season vegetative growth of the three sympatric *Platanthera* species in Yosemite renders surveys for this plant effective only from July to September when the plants are in flower or fruit.

KEY TO THE CALIFORNIA *PLATANATHERA* SPECIES

- 1. Flower white to cream; spur 1.5× or more the length of the lip, slender, cylindric *P. dilatata* var. *leucostachys*
- 1' Flower green to yellow, spur slightly longer to much shorter than lip; cylindric to variously inflated
 - 2. Viscidia presented on rostellum lobes to either side of spur orifice; column proportionally large, occupying about 2/3 of the hood formed by the dorsal sepal and petals, the connective very broad, the rostellum lobes prominent, widely spaced, and together with the stigma and connective forming a hemispherical chamber. *P. sparsiflora*
 - 2' Viscidia presented on rostellum lobes above spur orifice; column proportionally small, occupying less than half of the hood formed by the dorsal sepal and petals, the connective narrow, the rostellum lobes scarcely elevated, parallel, diverging, or converging, at most separated by a narrow slit and not forming a hemispherical chamber
 - 3. Leaves oblong to ovate-lanceolate, widely spaced along stalk, abruptly spreading from base to somewhat ascending, with internodes exposed and clearly evident; spur club-shaped to scrotiform; lip green (sometimes marked with small areas of fine reddish venation); scentless. *P. stricta*
 - 3' Leaves lance-elliptic to linear elliptic, clustered at base of stalk, ascending to gradually arching from base, with long-sheathing leaf bases mostly obscuring internodes; spur slender to scrotiform; lip yellowish; pungent-scented
 - 4. Spur <0.5 × lip length; saccate to scrotiform; lip bright yellow, inflorescence glaucous; pungent musk scent *P. yosemitensis*
 - 4' Spur 0.8 to 1.4 × lip length; clavulate (-cylindric); lip greenish yellow, inflorescence not glaucous; sweet pungent scent or scentless *P. tescamnis*

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LITERATURE CITED

- ALPHA, T. R., C. WAHRHAFTIG, AND N. KING HUBER. 1987. Oblique map showing maximum extent of 20,000-year-old (Tioga) glaciers, Yosemite National Park, Central Sierra Nevada, California. Miscellaneous Investigations Series Map I-1885. U.S. Geological Survey, Reston, VA.
- AMES, O. 1910. The genus *Habenaria* in North America. Orchidaceae: Illustrations and Studies of the Family Orchidaceae. Fascicle IV. The Merrymount Press, Boston, MA.
- CHABOT, B. F. AND W. D. BILLINGS. 1972. Origins and ecology of the Sierran alpine flora and vegetation. Ecological Monographs 42:163–199.
- COLEMAN, R. A. 1995. The wild orchids of California. Cornell University Press, Ithaca, NY.
- . 1988. The orchids of Yosemite National Park. American Orchid Society Bulletin 57(6):609–623.
- GORHAM, J. R. 1976. Orchid pollination by *Aedes* mosquitoes in Alaska. The American Midland Naturalist 95:208–210.
- HOUSE, M. A., B. P. WERNIKE, AND K. A. FARLEY. 1998. Dating topography of the Sierra Nevada, California, using apatite (U-Th)/He ages. Nature 396:66–69.
- , ———, AND ———. 2001. Paleo-geomorphology of the Sierra Nevada, California, from (U-Th)/He ages in apatite. American Journal of Science 301:77–102.
- KIMBALL, S., P. WILSON, AND J. CROWTHER. 2004. Local ecology and geographic ranges of plants in the Bishop Creek watershed of the eastern Sierra Nevada, California, USA. Journal of Biogeography 31:1637–1657.
- LUER, C. A. 1975. The native orchids of the United States and Canada, excluding Florida. The New York Botanical Garden, Bronx, NY.
- MATTHES, F. E. 1930. Geologic history of the Yosemite Valley. Professional Paper P-0160. U.S. Geological Survey, Reston, VA.
- MILLAR, C. I. AND W. B. WOOLFENDEN. 1999. Sierra Nevada Forests: Where did they come from? Where are they going? What does it mean? Natural resource management: perceptions and realities. Pp. 206–236 in R. McCabe and S. Loos (eds.), Transactions of the 64th North American Wildlife and Natural Resources Conference. Wildlife Management Institute, Washington D.C.
- , R. D. WESTFALL, D. L. DELANY, J. C. KING, AND L. J. GRAUMLICH. 2004. Response of sub-alpine conifers in the Sierra Nevada, California, USA., to 20th-century warming and decadal climate variability. Arctic, Antarctic and Alpine Research 36:181–200.
- MULCH, A., S. A. GRAHAM, AND C. PAGE CHAMBERLAIN. 2006. Hydrogen isotopes in Eocene river gravels and paleoelevation of the Sierra Nevada. Science 313:87–89.
- RAUP, H. M. 1930. The pollinization of *Habenaria obtusata*. Rhodora 32:88–89.
- RAVEN, P. H. AND D. I. AXELROD. 1978. Origin and relationships of the California flora. University of California Publications in Botany 72:1–134.
- RYDBERG, P. A. 1901. The American species of *Linnorchis* and *Piperia*, north of Mexico. Bulletin Torrey Botanical Club 28:605–643.
- SHARSMITH, C. W. 1940. A contribution to the history of the alpine flora of the Sierra Nevada. Ph.D. dissertation. University of California, Berkeley, CA.
- SHEVIK, C. J. 2002. *Platanthera*. Pp. 551–571 in Flora of North America Editorial Committee (eds.) Flora of North America, volume 26, Magnoliophyta: Liliidae: Liliales and Orchidales. Oxford University Press, New York, NY.
- AND W. F. JENNINGS. 2006. A new *Platanthera* from the intermountain west. Rhodora 108:19–31.
- SMALL, E. E. AND R. S. ANDERSON. 1995. Geomorphically driven Late Cenozoic rock uplift in the Sierra Nevada, California. Science 270:277–280.
- STOCK, G. M., R. S. ANDERSON, AND R. C. FINKEL. 2004. Pace of landscape evolution in the Sierra Nevada, California, revealed by cosmogenic dating of cave sediments. Geology 32(3):193–196.
- , ———, AND ———. 2005. Rates of erosion and topographic evolution of the Sierra Nevada, California, inferred from cosmogenic ²⁶Al and ¹⁰Be concentrations. Earth Surface Processes and Landforms 30:985–1006.
- STOUTAMIRE, W. P. 1968. Mosquito pollination of *Habenaria obtusata* (Orchidaceae). Michigan Botanist 7:203–212.
- THIEN, L. B. 1969. Mosquito pollination of *Habenaria obtusata* (Orchidaceae). American Journal of Botany 56:232–237.
- WERNICKE, B., R. CLAYTON, M. DUCEA, C. H. JONES, S. PARK, S. RUPPERT, J. SALEEBY, J. K. SNOW, L. SQUIRES, M. FLIEDNER, G. JIRACEK, R. KELLER, S. KLEMPERER, J. LUETGERT, P. MALIN, K. MILLER, W. MOONEY, H. OLIVER, AND R. PHINNEY. 1996. Origin of high mountains in the continents: the southern Sierra Nevada. Science 271:190–193.